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The Hypothesis of Formative Stuffs*

BY T. H. MORGAN

It is with some hesitation that I venture to discuss the hypothesis of formative stuffs as used by Professor Goebel in his Organographie and in his recent papers in the Biologisches Centralblatt. But since for all questions connected with the regeneration of plants it is of great importance to have a clear understanding of what this hypothesis really means, I hope that I shall be justified in entering into a discussion of this question, although the hypothesis is applied by its present adherents rather to plants than to animals. Professor Goebel uses the word correlation to give a name to certain curious, connected changes in different parts of the plant. Almost without exception when he ventures to express an opinion as to the cause of this connection, he makes use in one form or another of the Bonnet-Sachs hypothesis of formative stuffs. These stuffs are imagined to be either organized or unorganized substances that flow in different directions. The cause of this flow is sometimes ascribed to the polarity of the tissues; at other times to the attractive power for such substances that certain parts are supposed to possess. These alternatives are, I believe, fundamentally different conceptions.

I have made bold to question this hypothesis of formative stuffs.† More especially in the case of animals I have tried to show that there is little or no evidence in favor of such a view. In the case of plants I admit that under certain circumstances the presence or quantity of certain materials, especially food stuffs, may play a part in regenerative processes. But even in plants, despite the high authority by which the hypothesis is supported, I am sceptical whether formative stuffs are the chief factors in the result in those cases where polarity is involved. Let us examine the hypothesis more carefully. Bonnet suggested, in 1745, that the development of a head on one end of a piece of the worm, *Lumbriculus*, and of a tail on the other end of the piece, is due to fluids that flow forwards and backwards respectively, and act on head-germs at the anterior end of the piece, and on tail-germs at the posterior end. The accumulation of the head-stimulating fluid at the anterior end of the piece is supposed to awaken the germ of a head that lies at the anterior end. Conversely the tail-stimulating fluid, accumulating at the posterior end of the piece, awakens there the germs of the tail. It is unnecessary to point out that both the assumption of head- and tail-germs, and also the forward flow of certain kinds of substances, and the posterior flow of other kinds of substances are entirely fictitious assumptions, which from our modern point of view would be more difficult to account for than the phenomenon of regeneration itself.

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† Morgan, T. H. Regeneration, 88-90. 1901.

Sachs made use of the same idea, but in a very different form. He thought that the development of shoot-buds and of root-buds depended on the presence of certain substances in the plant. In order to account for the development of the shoots at or near the distal end of the piece, and of roots at the proximal end, he further postulated that the shoot-forming substances flow upwards, and the root-forming substances downwards — in response to the action of gravity. Vöchting's careful and elaborate series of experiments showed that the results cannot be explained so simply. He believes that an inner organization, or polarity, is the main factor in determining the result. Later Sachs also laid more emphasis than he had done at first on this innate factor.

Goebel appears at times to advocate strongly the idea that the flow of substances in the plant is the cause of several of the phenomena of regeneration. At other times he applies the hypothesis in such a vague way and under so many forms, that depend on quite different principles, not clearly kept apart, that the explanation often appears quite confused.

In his account of his experiments with seedling plants he makes little use of the hypothesis. On the other hand, in his beautiful experiments with cuttings of the stem of *Bryophyllum* he speaks out strongly in favor of the view that the results can be best explained on the assumption of the flow of certain substances, or at least of their accumulation in the plant. He thinks that the results of the experiments with the isolated leaves of the foliaceous liverworts can be best explained without assuming polarity, which in turn he here supposes to be associated with the absence of fibrovascular bundles in the leaves. He ignores the well-known fact that in many of the algae, which are extremely simple in structure, the polarity is as strongly expressed as in the regeneration of the higher plants. Moreover, the unicellular animals and plants show well-marked polarity. At other times Goebel speaks of certain growing regions — apical buds or cells — as drawing on the general supply of certain substances, and by continually exhausting these inhibiting the growth of other buds less advanced or less fortunately situated. He does not, I believe, sufficiently discriminate between this possibility, and the other view of the direction of the flow itself determining the development of certain parts.

I shall try to keep apart the idea that the presence of some particular substance may be the immediate cause of the growth of a part, and the idea of the flow of particular substances in a given direction as the immediate cause of growth. Moreover, it will be well to discriminate between the two possible causes of the flow. The polarity itself is sometimes hinted at by Goebel as the cause that determines the direction of the flow. On the other hand we may suppose that the flow is always towards the region where less of the substance exists and from the region where more is present.

The theory of mobile stuffs was first invented to explain the phenomenon that we call polarity. It is especially this part of the theory that I contest. I do not deny that the presence of certain substances in a piece may determine its reaction, neither do I question that a flow of certain substances in definite directions in the plant takes place, but I suspect the real cause of the flow in a given direction is dependent on the presence of certain organs, where the substances are being used or changed into other substances. Let us take a specific case and make definite applications of these different points of view. If a piece of the stem of a willow-plant is cut off and suspended in a moist atmosphere (its leaves having been previously removed) with its apical end upward, it will be found that the buds near the upper end of the piece begin first to grow, and grow more rapidly than those below them.

The buds near the base of the piece may not develop at all. The reverse is true in regard to the roots. They appear only at the base of the piece.

On Sachs' original assumption the development of the leaf-buds at the upper end of the piece is due to the accumulation at the upper end of some substance that causes them to develop. The development of the roots at the lower end is supposed also to be due to the presence there of another kind of substance. Vöchting showed that when the piece is turned upside down practically the same result follows; namely, the shoot-buds develop at the distal end of the piece, which is now the lower, and roots at the proximal end which is now the upper. This and other experiments make it highly probable that external factors play a very subordinate rôle in the development.

Now Goebel, following Sachs, is also at times inclined to ascribe the results of this, or of similar experiments, to the flow of different substances in the piece in different directions, but the cause of the flow is now ascribed to an internal factor, namely, to the polarization of the tissues themselves. It is somewhat ludicrous to find that while the hypothesis of formative stuffs was first invented to explain the polarity of the piece, the polarity is now assumed in order to account for the flow of the stuffs. My first question then is this: Is there any evidence to show that the polarity of the piece determines the direction of the flow of substances in the piece? I should also like to ask, is there any evidence to show that after the removal of a piece the flow of substances in it continues in the same direction as when the piece was a part of the plant?

In the first place can we account for the regeneration of pieces of the stem by means of the presence of formative stuffs, without assuming them to flow in definite directions? Let us see where such an assumption will lead. We may assume that when the piece is cut off certain substances accumulate in it. The excess of these substances tends to start the development of the leaf-buds and root-buds. Let us further assume that those leaf-buds will begin to develop that are the youngest, and these will always be those nearer the distal end. As they develop they will, by using up the substances present, retard the development of the other buds that are less developed. But in the case of the roots, the second assumption would have to be reversed, since those that develop are the oldest root-buds.

In this analysis I have attempted to give an explanation of the results without making use of the hypothesis of a directive flow of the formative stuffs, but it is clear that while the explanation may appear to hold for the shoots, it breaks down when applied to the roots ; and, I believe, that whatever form the hypothesis takes it meets with inherent difficulties.

For example, let us take the application that Goebel has made in his attempt to explain the results of two different experiments with cuttings of begonia. He found that if his cuttings did not produce roots at the lower end of the stem, then the buds in the incisions of the leaves began to develop. He explains their development as due to the non-development of roots, and the consequent accumulation of some substance in the plant. But this will only account for the development of the roots of the plantlets on the leaves, and not for the leaves of the plantlets.

Conversely, he found by removing all the buds from a plant that the buds in the incisions of the leaf began to develop. This again he explains on the hypothesis that those substances that are generally used up by the growing points have accumulated, when these parts have been removed. This might appear to account for the development of the leaf-buds in the incisions of the leaves, but not for the rootlets. The hypothesis proves too much.*

My second question is this : May we not meet in these cases of regeneration with a phenomenon essentially similar to that which recent experimenters on the development of the non-fertilized animal egg have encountered ? Contrary to the opinion first expressed, that the parthenogenetic development was due to the entrance of certain fertilizing ions into the egg, it has turned out that almost any kind of stimulus may start some eggs to develop. Such different kinds of things as salt-solutions, sugar, cold, heat, and even shaking will start the development of the egg of the star-fish. May this not be also the case with the piece of the plant ? Will not any physical change affecting the germ start its development? But if this is the case the difference in the behavior of the distal and proximal buds still remains to be accounted for, and this is the main point now under discussion. If we should be tempted to supplement the first assumption by making use once more of the idea suggested above in another connection, namely, that the youngest buds will be the first to develop, we should still, as we have already seen, get into a difficulty in regard to the roots.

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* It is taken for granted here that the shoot- and root-forming substances are different.

I am of the opinion that the phenomenon of regeneration can not be explained by a purely chemical hypothesis. I suspect, at least, that certain physical conditions may be equally important. My meaning can be best illustrated by certain experiments that I have recently made with the tubularian hydroid, *Tubularia Mesembryanthemum.* This case is especially interesting in the present connection, because it is the only instance in modern times in which the hypothesis of formative stuffs has been applied to animals to explain regeneration. Moreover, hydroids react in many ways to external stimuli much like plants.

If long pieces of the stem of tubularia are cut off, and then the head or hydranth be removed from the distal end, it will be found that a new head develops in the course of twenty-four hours. This head appears at the distal end of the piece. After another twenty-four hours another head develops on the other, the proximal, end of the piece.

The stem as well as the hydranth-head of tubularia contains a red pigment. Before a new head develops at a cut end the same red pigment begins to appear in this region. Loeb suggested that this pigment is a formative stuff produced by the stem, and that its accumulation at the anterior end gives the stimulus for the formation of a new hydranth. Later Driesch also studied the regeneration of these pieces of tubularia, and observed that red pigment appears in great quantity in the fluid that circulates in the center of the piece. He thought that its presence might act quantitatively, and determine the kind of incomplete structures that short pieces of the stem often produce.

I have been able to prove that both of these suggestions are wrong, because in the first place the amount of pigment that develops in small pieces is much greater than that which was at first present. Second, the amount in the stem does not decrease, while that at the end is increasing; and third, the red pigment of the circulating fluid disappears, not by going into the forming wall of the new hydranth, but by being collected into a ball in its stomach. Stevens has shown that this ball is later vomited from the mouth. Thus the pigment hypothesis of tubularia has been disposed of. Let us now consider the experiments that bear directly on my main theme. I have just pointed out that two heads develop on pieces of the stem of tubularia, one twenty-four hours after the other. This delay in the appearance of the proximal head would be interpreted on the stuff-hypothesis as due to the distal head, that first develops, using all the available hydranth-forming material. It can be shown that this cannot be the explanation. First, if a thread is tied around the middle of the piece the development of the distal hydranth is not delayed, but the development of the proximal hydranth is greatly hastened. Second, if a piece is simply bent, the proximal head will develop almost as soon as the distal one. Third, short pieces (if not so small that the usual kind of development is interfered with) produce distal heads as soon as do longer pieces; thus showing that the amount of material in a long piece is more than ample to allow a hydranth to develop at each end at the same time. Fourth, if the two ends of a long piece are allowed to close, and if then the piece is cut in two, the development of the distal hydranth is hastened. We may conclude from these experiments that the delay in the appearance of the proximal hydranth is not due to the direction of the flow oɪ the formative substances, because when a long piece is simply cut in two the development of the proximal hydranth may be hastened. The delay is due, only in a very small degree, to the polarity, because if the piece is simply tied in the middle the development of the proximal hydranth is hastened. Neither can the delay be due to the amount of food-stuff available, because pieces much shorter than half of these long pieces produce distal hydranths as soon as do the longer pieces. The stuff-hypothesis fails to explain the facts from every point of view.

The results certainly suggest that some physical factor enters into the problem. It seems to me that whatever this physical factor may be, it is the same that we find acting wherever growth and the formation of new structures are taking place.

In my book, "Regeneration," I offered, as a pure conjecture, the suggestion that this physical factor expresses itself in the form of different tensions in the living tissues. Goebel asks whether such a conception puts the question in any clearer light than before. I am inclined to think that the idea is not entirely worthless, and it should not be forgotten that I pointed out, as emphatically as possible, that the view is only conjectural and must be tested by further work. It was offered as a possible working hypothesis, and it is unfair to treat the suggestion in any other light. If the view appears too vague it can be given a more practical form by assuming that the differences in tensions are simply the outcome or expression of osmotic changes, which are themselves in turn the result of the presence of certain chemical substances present, or being produced in the organism.*

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* Since the above was written Matthews has suggested that my tension-hypothesis may be an expression of the electrical conditions in the piece; in short, that "polarity" is an electrical phenomenon; possibly, I may add, due to the movement of ions.